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Species Richness and Stand Diversity in Relation to Site and Succession of Forests in Sarawak and Brunei (Borneo)

by

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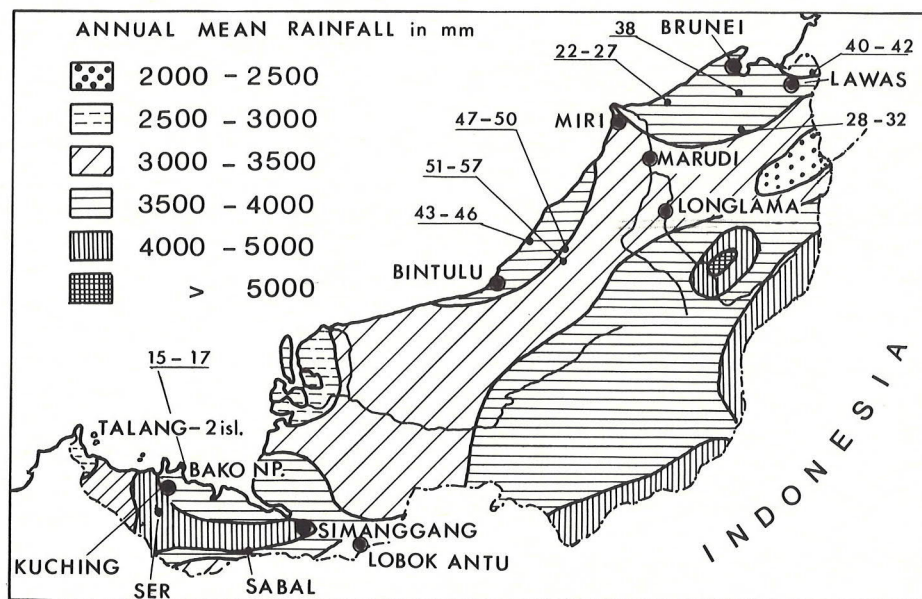
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1. INTRODUCTION

Sarawak lies in an optimum area of humid-insular equatorial climate and in the centre of the richest floristic region of the world (GOOD 1964; BRÜNIG 1972 a). The flora as a whole and individual forest communities and stands are distinguished by a great richness in species. The probable causes for this floristic richness have been most aptly discussed by ASHTON (1969).

The combined effects of a strong tendency to endemism and of a variable and diverse, but climatically continually favourable environment provided the extraordinarily large niche hyperspace which has become occupied by the great multitude of tree species, each with an apparently narrow ecological range. These many tree species form communities on the various site types (BRÜNIG, in print) which differ distinctly with respect to species composition, stand structure and physiognomy. These differences seem to correlate with site conditions. In some cases this is clearly obvious. In others, close scrutiny is needed to detect it. The existence of narrowly defined but not clearly delimited types and the consistent occurrence of species and forest types on certain site types suggest that the environment and the interaction between species produces a vast niche hyperspace in the equatorial lowland forest with individually narrow niches for which a species probability of occurrence is greater than for other regions of the niche space.

A vast niche of space with many slightly different, narrow ecological niches can only be available if there is no excess or deficiency of a climatic factor severe enough to mask the minor differences of the micro-sites. BAILLIE'S (1972) calculated estimates in fact suggest that the vegetation on deeper soils with larger water holding capacity is



Map 1. Locations of sample plots and of the Sabal sampling area.

rarely or, particularly further inland, practically never subject to moisture stress. Conversely, periods with severe moisture stress occur regularly on soils with lower water holding capacity in the rooting zone. This is particularly noticeable on the drought-sensitive Kerangas soils where ecologically effective droughts are frequent (BRÜNIG 1969 and 1971). Consequently, the number of species would be reduced to the depressed level of niche space. Similarly, the strongly fluctuating water table and the relatively great uniformity of site in the peaty Kerapah and in the peat swamps would work in the same direction and be responsible for the poorness of tree flora on these sites.

2. SPECIES RICHNESS OF THE TREE FLORA

2.1. Total number of species

The total number of tree species in Sarawak may be estimated from the sample plots data given by ASHTON (1964) for mixed Dipterocarp forest (MDF) and BRÜNIG (1968) for Kerangas and Kerapah forest (KF), and from the list of peat swamp forest (PSF) species by ANDERSON (1964). The frequencies of species in a sufficiently large population approach a normal distribution if they are plotted over frequencies of individuals which are divided into octaves of numbers of individuals (PRESTON 1948; BLACK et al. 1950; PIELOU 1969). Any sample of a mixed population will include most of all common species but fewer of the rare species. As a result the distribution is curtailed or veiled on the left. The total number of species may be estimated by extrapolating the distribution to the left. This requires that the mode is on the right of the veil line.

Table 1. Number of tree species in classes of octaves of numbers of individuals.

Locality	Forest type**	Soil type	Sample plot no.	Total number Species	Indiv.	<1	1-2	2-4	4-8	8-16	16-32	32-64	64-128	128-256	256-512	512-1024	1024-2048
SARAWAK																	
Bako N.P.	sekundärer Kerangas	MHP	17	116	1 094	> 20,5	34,5	14,5	17,5	18	4	3	-	-	-	-	-
Badas	Kerangas	DHP	22	108	636	> 12	25,5	25	24,5	12	5	4	-	-	-	-	-
Badas	Kerangas	MHP	23	93	916	> 16	25,5	20	19	10,5	6	5,5	1	-	-	-	-
Badas	Kerangas	GHP	27	90	793	> 11	11,5	17,5	11,5	18,5	13	7	-	-	-	-	-
Bumbong rumah	Kerapah	PB	40	69	832	> 14	18,5	14,5	9	5	6	-	1	-	1	-	-
Niah-Jelalong	Kerangas	GWP	47	188	839	> 25,5	44,5	47	41	21	8	1	-	-	-	-	-
Niah-Jelalong	Kerangas	RYP	50	162	581	> 30,5	44	39,5	32	11	3	1	-	-	-	-	-
Merurong Plateau	Kerapah	PB	57	65	668	> 10	12,5	13	9,5	5	7	8	-	-	-	-	-
Sarawak	Sum v.55 SP	-	1-57	774	42 436	> 62	92,5	89	93	87	99,5	87,5	78,5	50	24	10	1
Teté*	Terra firme	RYP	-	79	230	> 21	28	17,5	4	6,5	2	-	-	-	-	-	-
Belém*	Terra firme	RYP	-	87	423	> 16,5	24	24	10,5	5	4	3	-	-	-	-	-
British Guiana*	Mora	Lehm	I	59	462	> 11	16,5	10	6	9,5	3	2	1	-	-	-	-
	Moraballi	Lehm	II	68	460	> 12,5	17,5	12,5	13	7	4,5	1	1	-	-	-	-
	Ocotea	Sand	IV	94	773	> 15,5	21	19,5	17,5	9	3	6,5	2	-	-	-	-
	Eperua	Sand	V	71	919	> 11,5	15	11	10,5	11	8	1	1	2	-	-	-

*Data for Teté, Belém and British Guiana from Black et al. (1950, p. 424).

**For general descriptions of the forest vegetation of Sarawak see ASHTON (1964) and BRÜNIG (1972 a).

Table 1 shows the distributions for trees with a diameter of more than 1 cm in 8 sample plots of 0,2 ha each, on medium and deep humus podzol (MHP, DHP), ground-water HP (GHP), peat bog (PB), grey-white podzolic (GWP) and red-yellow podzolic soil (RYP). The distribution in the single plots is obviously truncated in the modal octave or to the right of it. It is therefore probable that less than 50% of the species have been sampled which occur in the population represented by any of the plots. The same is true for the much larger 1,0 ha in Tefé and Belem and 2,49 ha in plots in Latin America in which only trees with a diameter of more than 10 cm were enumerated. Only the distribution for all 55 Sarawak KF plots combined indicates a peak to the right of the veil line (Fig. 1).

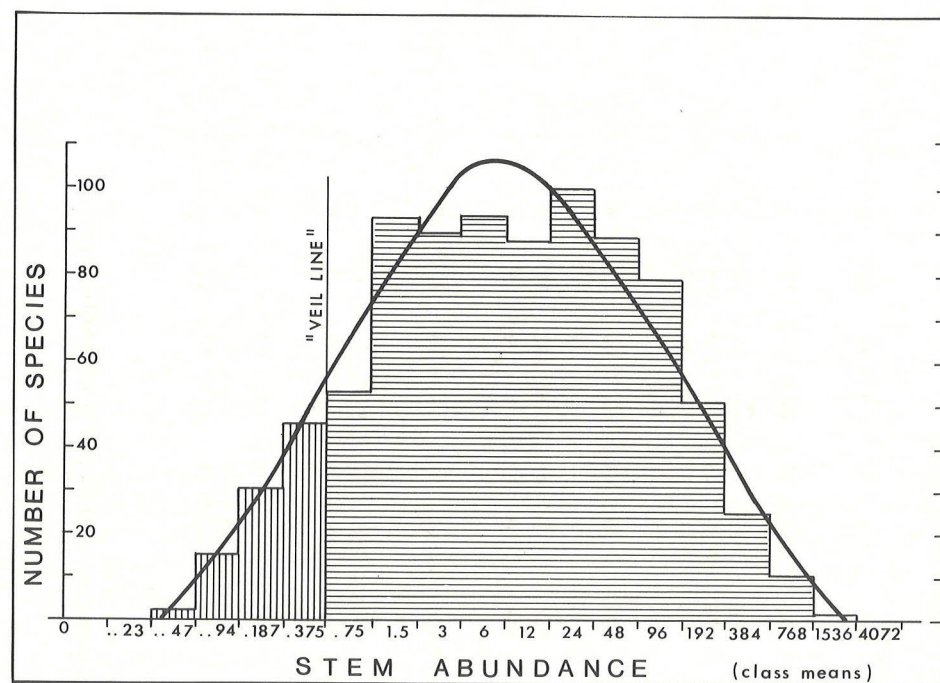


Fig.1. Log-normal distribution of number of tree species over octaves of abundance of individuals in 55 sample plots in Kerangas and Kerapah forest in Sarawak and Brunei.

The area beneath the extrapolated tail equals 82 species. The total number of tree species in the KF represented by the sample plots is then $774 + 82 = 856$. My extensive botanical collection of Kerangas and Kerapah series, housed in the Kuching herbarium, includes 849 tree species in 428 genera. This is satisfactorily close to the estimate.

ASHTON (1964) recorded tree species with a diameter of more than 10 cm in two sample areas of MDF in Andulau (420 species) and Belalong (472 species) in Brunei. Only 134 (17.4%) species were shared by the two areas. The total species number may be estimated by comparing ASHTON's figures for species and individuals with those from areas which I enumerated in KF and with the total number of Kerangas species. According to this comparison the total number of species in the MDF of Sarawak and Brunei seems to lie between 1800 and 2300. Of these, 220 are known to be shared with KF. ANDERSON (1963) listed 234 tree species in the PSF which represent at least 90% of the total tree flora. 146 of these are shared with KF. No species is shared by MDF and PSF which does not also occur in KF (BRÜNIG 1968 b). The estimated total number of tree species in the three forests is then

Mixed Dipterocarp forest	1 800 – 2 300
Kerangas and Kerapah forest only (56% of 860)	480
Peatswamp forest	260
	2 540 – 3 040

Adding species which are exclusive to forest vegetation on mangrove, ultra-basic rock, limestone and montane sites gives the estimate of the total number of tree species in Sarawak and Brunei as between 2 800 and 3 300.

2.2. Species richness in relation to site

ASHTON (1964, p. 39 and Figs. 10 – 21) found that in MDF the species complement, total number of species, shape of species-area curve and the ratio of species to individuals differed between stands which were arranged along an ecological gradient from more xeric to more mesic sites. Comparable trends were observed by BRÜNIG (1968, pp. 78 – 83, Table 8) in Kerangas forest. 55 Kerangas forest stands were ordered by SORESENSEN's similarity quotient. Species richness per area and per 100 individuals differed along ecological gradients related to dryness, drainage and nutrient levels of the site. Stands on comparable sites had somewhat more species in the north than in the south of the area. The reason for this is as yet obscure. The more equable climate in the north may be one reason.

If we assume that not only species richness influences the pattern of species richness on a site, but also niches which are defined by limiting site factors, it would follow that the steepness of the species-area lines and the scatter of observed values about them should increase more markedly than the number of species as one proceeds from poorer to better sites. The reason is that on the latter, niche-hyperspace is less severely restricted.

The species area lines of a selection of stands representing the range of site conditions in Kerangas are shown in Fig. 2. The soils are secondary MPH (SP 17), dry shallow HP (SP 15), dry MHP (SP 43), moist MHP (SP 30) and deep, loamy RYP in the

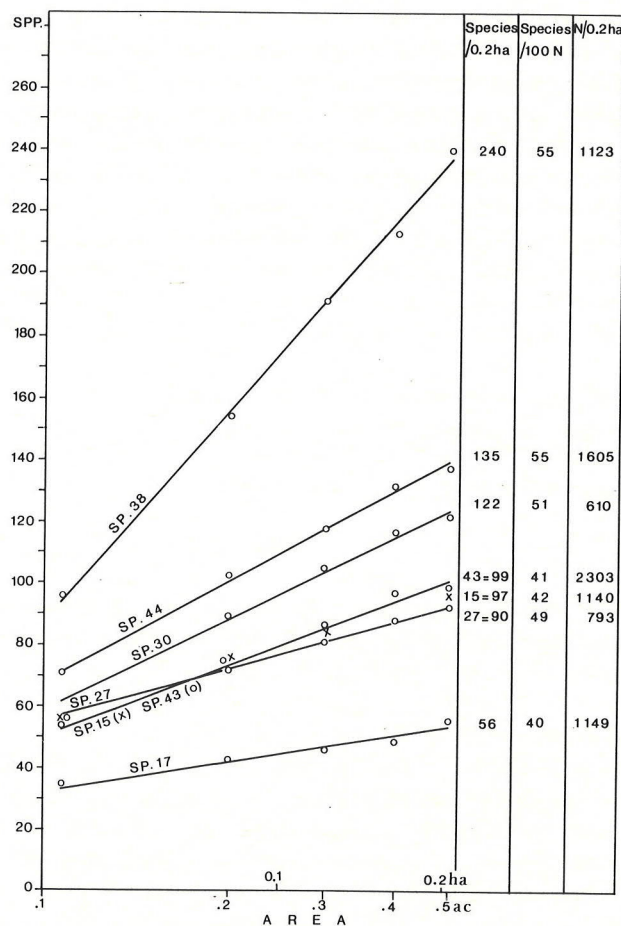


Fig. 2. Species area lines for selected single sample plots in Kerangas forest, trees of diameter more than 1 cm, total number of species, number of species per 100 individuals and number of individuals per plot. SP = sample plot.

transition to MDF (SP 38). The slope of the species-area line is determined by the ratio of initial number of species to total number of species. The slope expresses the rate of species additions as the area is enlarged. The slope of the lines increases with the improved soil conditions. The ratio of initial species number in the poorest and the richest primary forest plot is 1 : 1,8. The ratio of number of species in 100 consecutive individuals is 1 : 1,3. This compares with a ratio of total number of species of 90 : 240 = 1 : 2,7, and a corresponding ratio of the tangent of 1 : 5,7. Comparison with the densities (N/0,2 ha in the last column of Fig. 2) shows that species richness and rate of species addition are not related to density. The tangent of the species-area lines and the mean variation coefficients were calculated for 27 of the 55 stands.

The mean variation coefficients were 0,9% on peat bogs (4 stands), 1,4% on HP and GWP soils (17 stands) and 2,7% on deep RYP and bleached sandy clays (6 stands). The mean species ratio between poorest and best site is 1 : 2,2 for one recording unit and about 1 : 3,5 for whole plots (5 units). The corresponding ratio of the coefficients of variation is 1 : 5,7. The variability, therefore, increases more rapidly than the number of species. SPEARMAN's rank coefficients for number of species, slope of species-area line, variation coefficient and sequence along ecological gradients proved that the variation coefficient does not depend on the same factors as number of species and slope of line. It appears to be related to site heterogeneity and is independent of the total number of species ($r_s = 0,312$) and of the tangent of the species-area line ($r_s = 0,353$) (BRÜNIG, in print).

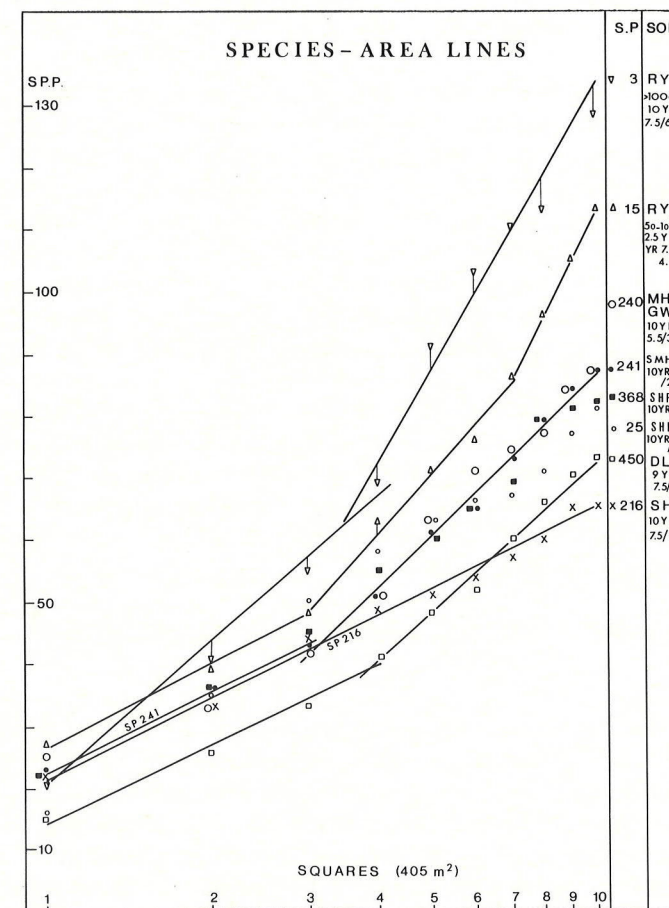


Fig. 3. Species-area lines for sequences of 10 square chains on different soil types in Sabal F.R., trees more than 10 cm in diameter. DLS = deep clay latosol; RYP = red-yellow podzolic loam; SHP = shallow humus podzol; MHP = medium humus podzol; GWP = grey-white podzolic soil. Munsell colour notations refer to 20 cm soil depth. SP = sample plot number, starting point of transect.

Fig. 3 shows the same general trends of the species-area lines and the species : individual ratios in transects of 10 recording units (405 m² squares) in a 20,2 ha sampling area containing KF and MDF on a moderately heterogeneous site in Sabal F.R., south west Sarawak. The initial number of species in the transects is not very different, except for transect 450, but widens as additional units are added. Transect 216 is on SHP. The site is relatively homogeneous (see Fig. 4, right side). The species-area line is reasonably straight and closely fitting. With increasing depth and colour of the soil rooting zone, the slope of the lines steepens and the effect of soil heterogeneity becomes increasingly more evident, shown by the tendency of the lines to bend upwards such as in SP 15 and 3 in transitional forest to MDF. The apparently aberrant position of transect 450 on a reddish-yellow clay soil in MDF is caused by the extreme dominance of one species, *Dryobalanops beccarii* Dyer, Dipterocarpaceae. This species regenerates profusely below parent trees and shows a strong tendency to clustering on shallow but moist clay and sandy soils.

The shape of the species-area lines in Figs. 2 and 3 suggests that on the shallower soils, differences in soil conditions are much less effective in providing niche space than the site differences on deeper soils, which are characterised by a more balanced water regime. The immediate response to increased soil depth is illustrated by transect SP 241 in comparison to SP 216 (Figs. 3 and 4). In SP 241 the species-area curve is almost straight to square 244. In SP 245 the soil is deeper and better drained, and more new species occur. In the squares 248 and 249, soil chroma deepens and more new species occur. In transect SP 216, which starts on a slightly peaty site, soil depth and chroma hardly change from 218 to 225 and the species-area line more closely fits a straight line.

Generally, the strong curvature in the transition to MDF agrees with the trend in ASHTON's (1964) species-area lines from MDF proper. It demonstrates the generally greater number of species and indicates a more effective niche formation in MDF than in KF. There is a continued addition of a greater number of species than would be expected if stands were homogeneous, species were randomly distributed, and neither site nor time acted effectively on the species occurrence.

3. DIVERSITY IN RELATION TO SITE AND STAND DEVELOPMENT

3.1. Choice of statistics

Frequently, diversity is simply equated to species richness expressed as species content of a sample. A recent example from tropical rain forests is given by TSCHIRLEY et al. (1971). This is unsatisfactory, because it ignores the distribution of individuals (equitability) within species. More widely applicable and informative are statistics which combine species richness and equitability. A general review of the subject is found in PIELOU (1969). Information from measures of diversity appears particularly suited to complex-structured equatorial forests, but the computational load is rather heavy. The relatively simple formula of BRILLOUIN (1962), which measures diversity in bits of information per plant, has been adapted for a comparison with the McINTOSH (1967) index of diversity. The latter has the advantage of simplicity of computation, large degree of inde-

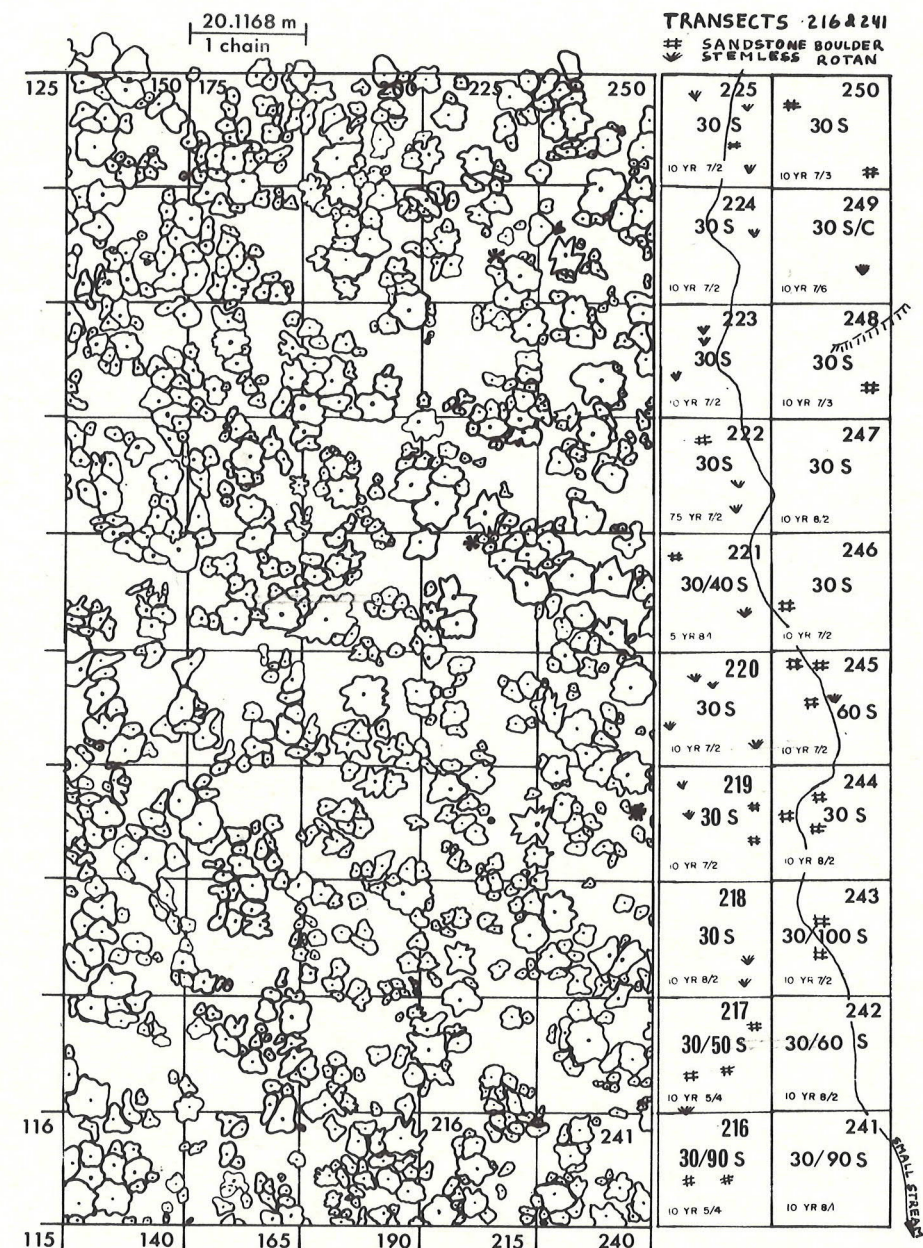


Fig. 4. A section of 50-square units of the sampling area (500 units = 20,2 ha) in Sabal F.R. Transects SA 216 and SA 241 run along the right (units 216 to 225 and 241 to 250). Parts of transects SA 240 and SA 25 enter the left part of the section. The crown projection is only of the top-canopy trees. These trees are the roughness elements which are used for calculating the estimated aerodynamic surface roughness. Some site factors of transect SA 241 are shown at the right. The serial square number is at the top. The number in the centre of each square unit is the soil depth to underlying sandstone in cm; S = sand, C = clay. The figure at the bottom of each square is the MUNSELL soil colour notation at 20 cm depth below soil surface (A₀ horizon at base of main rooting zone). Rotan is a vernacular name for palms of the genera *Calamus* and *Daemonorops*.

pendence from sample size, direct ecological relevance, and suitability for testing the significance of means and differences. In addition, dominance patterns are demonstrated by dominance-diversity curves (WHITTAKER 1965). Finally, an integrating index was constructed to express the combined effects of species richness and pattern of vegetation and site.

3.2. Diversity according to formulas of McINTOSH and BRILLOUIN

McINTOSH uses the abundance per species in the stand to express the diversity. In the formula (see Fig. 5) N is the number of individuals in the sample and n the number of individuals per species in abundance class k . For 100 individuals and 10 species, the maximum value of the index is 0,88, if each species has 10 individuals. The minimum index value is 0,10, if one species is represented by $n=91$ and the other 9 each by $n=1$. The index values range from 0 (all individuals of one species) to 1 (each individual a separate species). The value is greater for evenly distributed species and smaller if the species differ in abundance (n). The squaring of abundance makes the index especially useful for stands with much small-scale variation in dominance pattern. This is the case in the forests of Sarawak which represent a continuum with a varied pattern of association complexes, in which the presence of many late stages of succession at micro-scale (COUSENS 1956) and micro-site differences play an important role (ASHTON 1964; BRÜNIG 1968).

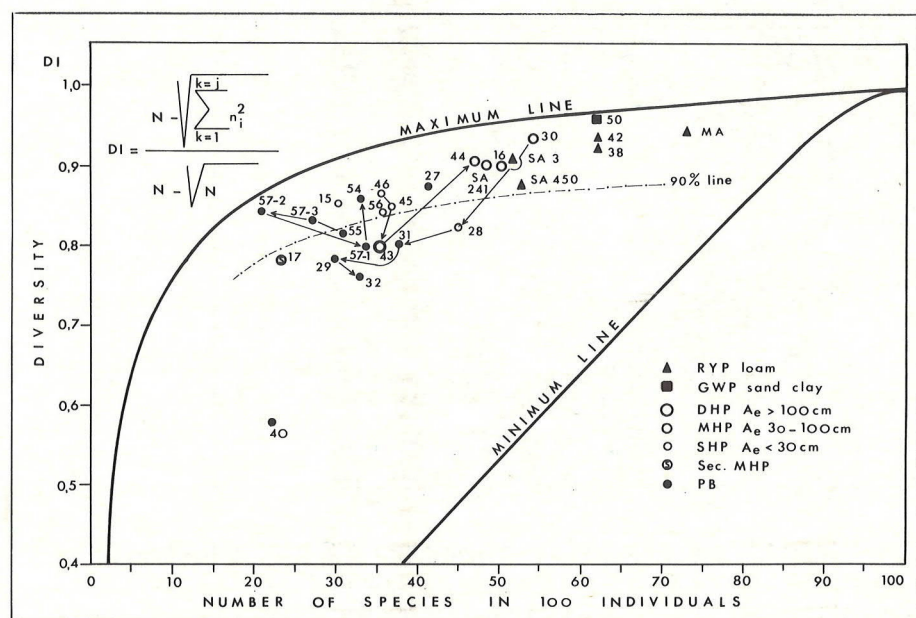


Fig. 5. The values of the McIntOSH (1965) index of diversity for 100 stems of diameter more than 1 cm. Arrows indicate catena or successional relationships. N = number of individuals (100), n = number of individuals in each species. MA = sample from the biomass plot near Manaus.

The sample plots were regarded as individual stands. Series of 100 individuals were randomly selected from the field lists. The index values for a selected number of stands are shown in Fig. 5. SP 50 on a deep, moist GWP near the crest of a tertiary syncline at an altitude of 175 m has the greatest number of species and the highest degree of diversity in relation to the maximum possible. SP 42 lies on the upper slope of an undulating tilted sandstone plateau at an altitude of 700 m. SP 38 is on the lower end of a synclinal slope at an altitude of 10 m. The soil in the last two plots is a RYP in the transition to MDF. The vegetation in all three plots is transitional to MDF, with increasing tendency to single species dominance from SP 50 (*Agathis borneensis* Warb., 8% of G) to SP 42 (*Lithocarpus cyclophora* (Endl.) A. Camus, 12,7% of G) to SP 38 (*A. borneensis*, 15,6% of G). The other stands on RYP soil are SA 3 and SA 450 which have fewer species due to a larger minimum sampling size and a lower relative diversity due to the gregarious occurrence of some Dipterocarp species.

In KF proper, the largest number of species and the highest relative diversity values occur in stands on HP with balanced water supply (SP 30, 16, 44). The lowest value in KF occurs in SP 40. This stand is strongly dominated by tall, slender and dense *Dacrydium cf. beccarii* Parl. in the top storey and two species of Sapotaceae in the D and C storeys. The soil is a 3 m deep peat on an early pleistocene peneplain remnant perched on a tertiary sandstone plateau at an altitude of 680 m in northern Sarawak (Map 1).

The sequence SP 55 to 54 represents the peat bog formation under KF on a tertiary sandstone plateau at an altitude of 700 to 1 200 m in the interior of central Sarawak. SP 57-2 has a small number of species but a high degree of diversity. This stand is in an unstable transitional zone in the mid-phase of peat bog formation. The series starts in closed high forest at the periphery of the bog (55 and 57-3) and proceeds to open pole-wood land in the centre (57-1). Instability of the stand seems to eliminate any strong dominance pattern which is evident on either side of the position of SP 57-2. The relatively low diversity value in the low open stand is caused by a great abundance of a few species in the C and D layers. The diversity value of this open stand would be much larger if the minimum sampling size were lowered to include ground vegetation. SP 54 on a blanket peat of the summit slope at an altitude of 1 125 m above SP 57 has a relatively high diversity value. This is due to a relatively rich, tall shrub layer, in spite of the high degree of dominance of one species (*Gymnostoma nobile* Johnston, Casuarinaceae) in the B layer. An increase of diversity for trees and shrubs together with simultaneous decline for trees alone is characteristic for open stands in peat bogs. REINERS et al. (1971) report similar changes for a successional series from alder-willow thicket through stages of spruce-hemlock communities to muskeg in Alaska.

The series SP 30-28-31-29-32 across a complex of mid-pleistocene terraces is another example of the change of diversity in the course of topogenic paludification. SP 30 lies on a MHP on the younger, well-drained level (altitude 165 m), SP 28 near the rim of the following older level (altitude 185 m) with a more imbalanced water regime. The terrain on the top of the older level forms a broad, flat depression, more than a kilometer wide, which is poorly drained. In SP 31 (altitude 183 m) waterlogged conditions

initiate peat formation. This stand and the following SP 29 have the heaviest waterlogging at the edge of the raised peat bog. The stand in SP 29 is in an unstable transition, similar to SP 57-2, but its diversity is much reduced by the effects of extreme waterlogging. Further on, peat accumulation has raised the surface level well above the average water table. Consequently, surface drainage is improved and more species can occur. As a result, SP 32 (182 m altitude) has more species but its diversity is still very low. This is due to the occurrence of peat swamp species such as *Shorea albida* Sym., *Combretocarpus rotundatus* (Miq.) Dans. and *Gonystylus bancanus* (Miq.) Kurz, which tend to be gregarious on raised peat.

The series SP 46 – SP 44 gives an example of the diversity pattern along the coastal terrace catena. The sequence starts in SP 46 on a recent beach terrace with mesic GHP. The stand is weakly dominated by *Shorea materialis* Ridl. in the A layer, and more strongly by *Ganua curtisii* (K. et G.) H.J. Lam in the B/C layers. The next stage is the slope which leads to the next higher terrace level (SP 45). The soil is a well-developed MHP. The dominance pattern is strengthened by the occurrence of *A. borneensis*. This species attains strong dominance in SP 43 on the top of the 6 m terrace level (56,3% G). The site is relatively xeric due to the excessively drained DHP soil and the strong exposure to sea breezes. This favours the microphyll-notophyll, deeply tap-rooted *A. borneensis* in the A/B layers, and distinctly microphyll-nanophyll and sclerophyllous species of the genera *Hopea*, *Garcinia*, *Eugenia* in the C/D layers. The next stand (SP 44) is on a moist MHP in the centre of the highest terrace level (altitude 14 m). The site is mature, and paludification is just beginning in hollows. The water regime is, on the whole, balanced. Consequently, the number of species is larger (Fig. 2) and the diversity markedly higher (Fig. 5). It is likely that further development will lead to peat bog formation as in the series SP 30–32.

For comparison, 6 samples were drawn from the population of the biomass sample plot which Dr. KLINGE enumerated in terra firme forest near Manaus, Amazonia, and which is described elsewhere in this issue. The site and forest correspond to MDF in Sarawak. The same minimum size requirement applied as in the Sarawak samples. Species richness ranged from 17 to 29 per 100 individuals, and index values from 0,802 to 0,841. This puts the stands within the cluster formed by high-altitude peat bog series (SP 54 to 57-2 in Fig. 5) and low-altitude SHP (SP 15) in Sarawak. The flora is poorer and the diversity lower than in forests on comparable soils in MDF in Sarawak. The lower diversity indicates a smaller degree of integration, for which the reasons are as yet obscure. lowering the minimum size to include small saplings (height 1 m) increased species richness very strongly to 71 per 100 N, but the DI value remained relatively low at 95% of the maximum possible (SP MA in Fig. 5).

The contribution to the stand structure by trees in a mixed tropical forest is less adequately measured by their abundance (number of individuals) than by their basal area cover. Basal area is also a more adequate measure of ecological success. Basal area was therefore substituted for number of species in the McIntosh index for the stands along the terrace series SP 46 to 44 (coastal terrace catena with progressing podzolization)

and SP 30 to 32 (older inland terrace catena with paludification). In both cases, basal area accentuates the dominance pattern in the mid-phases with the largest environmental stresses (Fig. 6 a). On the inland terrace series, the position of SP 32 is practically unchanged, while SP 28 has gained and SP 30 has lost. This indicates that in the relatively juvenile phase of SP 30 a few species contribute a greater portion to the stand biomass than to the number of individuals. This tendency is weaker in the more mature phase of SP 28. The dominance of few species is again more evident in the stands with more severe site conditions (SP 31, 29).

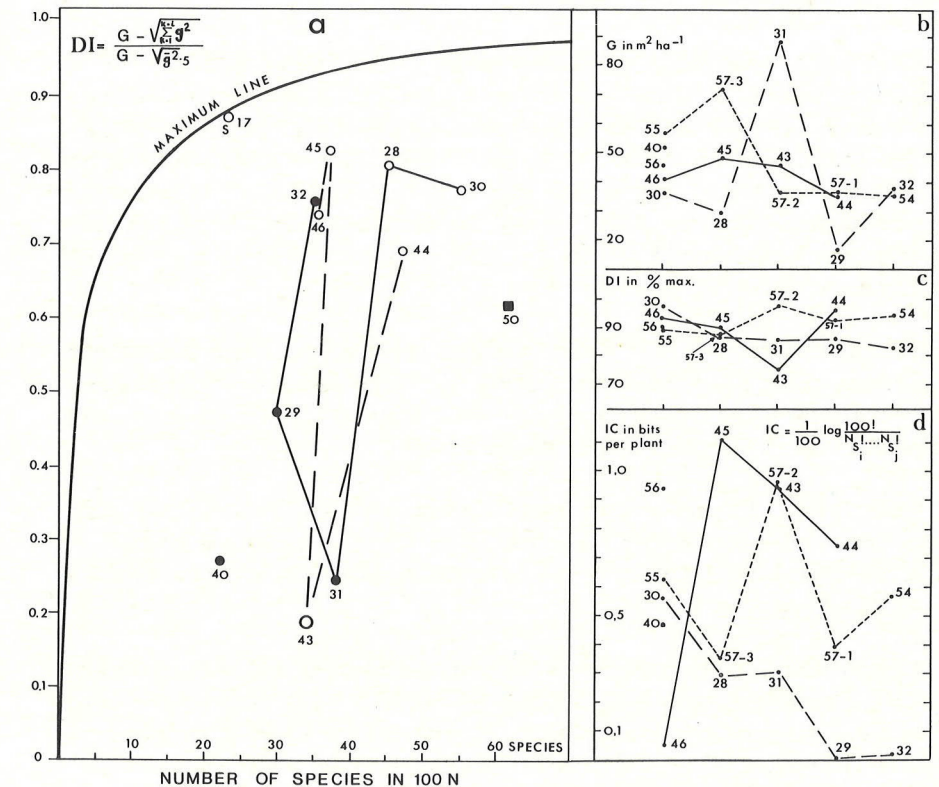


Fig. 6. Change of structural features along catenas and successional series:
a) Modified McIntosh index of diversity for the coastal (46) and inland (30) terrace catena and SP 17, 40 and 50. G = basal area of 100 individuals, g = basal area for species.
b) Basal area per hectare. 50 = catena and peat bog series on tertiary plateau.
c) McIntosh index of diversity for N in per cent of maximum value.
d) Average information content in bits per plant.

This pattern of changes of position is almost identically repeated in the sequence SP 46 to 44. The very low value of SP 43 illustrates the peculiar ecology of a DHP soil with a hardpan at 170 cm depth. During brief droughts, the pan improves water supply to deep-rooting species. This gives a decisive advantage to *A. borneensis*, which consequently strongly dominates the A/B layers. The distinctly separated C₂/D layers are very dense and the species appear from soil pit inspection to be shallow-rooted. This means that the species are exposed to strong stresses during drought, since radiation is relatively high but available soil water supplies are low. The strong dominance of nanophyll, distinctly sclerophyll species in this stratum would therefore appear to be a physiognomic adaptation to the exacting environment. The overall result is the very low value of the index of diversity of basal area cover.

SP 40, on the high-altitude peneplain remnant, retained its low position. The slenderness of the trees in all storeys of the stand reduces the difference between the effects of number of trees and basal area. SP 50 ranks high in Fig. 5 but relatively low in Fig. 6 a. In this stand a few scattered large *A. borneensis* tower above a distinctly separated highly diverse C layer. The original McINTOSH index is relatively insensitive to this type of dominance pattern. Consequently, the stand ranks high. The modified index gives greater weight to the high coverage of *A. borneensis*. Consequently, the stand diversity value is reduced.

The old secondary KF in SP 17 on a secondary MHP reaches nearly 90% of maximum diversity in Fig. 5 and almost 100% in Fig. 6 a. This is caused by a high frequency of species in the C and D layers, and by the small diameter of species in the A and B layers, which reduces their effect in the modified index.

Stand diversity is apparently not associated with stand basal area stocking. Basal area stocking culminates more (SP 31) or less (SP 45/43) pronouncedly in the mid-sections of the successional series (Fig. 6 b). The relative DI (Fig. 6 c) does not show a corresponding trend.

The information content measure of diversity declines generally with increasing site and stand maturity (Fig. 6 d, series SP 46–44 and SP 30–32). The very low value in SP 46 is due to immaturity and correspondingly intense dominance pattern in the B/C layers. The peak in SP 57–2 is related to the unstable state of stand and site. The very low values in SP 29 and 32 are caused by a high dominance of invading peat swamp species. Generally, the trends in Fig. 6 c agree well with the positions of the stands in Fig. 5 for series SP 55–54 and SP 30–32. The agreement is less close in the series SP 46–44. The reason is obscure, but might be related to the greater sensitivity of the information measure to the dominance pattern. An interesting example of close correspondence in structural features in spite of structural dissimilarity are the positions of SP 45 (MHP on a coastal terrace) and SP 56 (MHP on a tertiary plateau at an altitude of 735 m). Both stands agree quite closely in total stand basal area (48,0 and 46,6 m²/ha), basal area distribution of leading species, number of trees (10 605 and 9 205 N/ha), DI percent of maximum (90,4 and 89,2%) and average IC (1,11 and 0,994). Their floristic

composition, however, is very dissimilar. SP 56 is one of the reference stands (X = 100) in an ordination of the 55 kerangas stands, in which SP 45 is positioned at X = 443.

3.3. Diversity according to the dominance-diversity curve.

The ecological importance of a tree species for the stand may be measured by its contribution to the number of individuals, basal area, biomass, or productivity. Basal area has the advantage of being a reasonably good measure of the ecological success of a species, and is much more easily obtained than biomass or productivity. The per cent basal areas of the species in selected stands were plotted in descending order on semi-logarithmic paper in the manner described by WHITTAKER (1965). The resulting dominance diversity curves (DD curves) would be very flat if basal area coverage among species were randomly distributed. This condition corresponds to a high basal area diversity and a random pattern at larger scale of species distribution over the stand area. A moderately steep sigmoid curve results if relatively few species are very successful and contribute a large share to the basal area. Correspondingly, very few species would be very unsuccessful. The majority of species are intermediate. It is chiefly these species which contribute to the stand diversity. The sigmoid curve corresponds to PRESTON's general lognormal distribution described earlier. WHITTAKER (1970) suggests that this form of distribution indicates that the relative importance of the species in a species-rich stand is determined by a great number of independent variables, which affect the various species differently. Accordingly, the extent of the ecological niche space of any species in a stand is determined by a multitude of interacting environmental factors, acting on the species in a specific situation of competition from other species.

A still steeper slope on the curves would indicate that niche space is occupied by mutual exclusion. The most successful species occupies a certain proportion of available niche space, excluding all other species to the residual space. This is then divided among the remaining species, the most successful species again occupying a certain proportion of the residual niche space first. This goes on until all available space is distributed among available species. If a few species are very strongly dominant, the initial slope will become very steep, leaving space for only a few intermediates, which causes relatively more species to be very rare. This type of curve approaches the geometric series and is characteristic for stands in a severe environment, such as subalpine (WHITTAKER 1970, p. 28), or subarctic (REINERS et al. 1971) sites.

The shape of the curve is not independent of sampling size. This applies to area as well as to minimum sampling size of trees. The relatively steep-sloping curves 57–3 to 57–1 (Fig. 7) and their less steep combined curve 57 (Fig. 8) agrees with WHITTAKER's (1970, p. 29) statement, that "a lognormal form appears for a mixed sample, even though the curves for individual communities might approach the form for the geometric series". The slope of the curves steepens from SP 57–3 at the edge to SP 57–1 in the centre of the raised bog. This happens in spite of a lesser basal-area dominance of the leading species in the latter stand, and reflects a lower diversity in the intermediate storeys. SER 1–4 is a pole stand with few emergent trees on shallow peat over strongly corroded, hard limestone on a hill in the lowlands. Both water and nu-

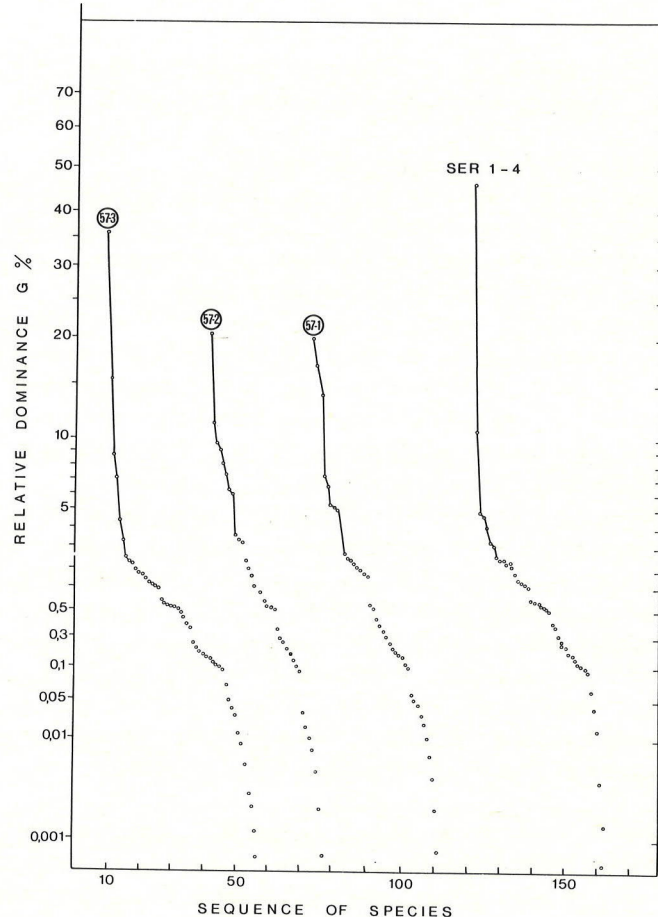


Fig. 7. Relative Dominance-Diversity curves for three stands along the peat bog gradient from the edge (57-3) to the centre (57-1) of a raised bog on a sandstone plateau, at an altitude of 730 m. SER 1-4 is a stand on dry peat on a limestone Karstkegel at an altitude of 60-130 m.

trient deficiencies are severe. The shape of the DD curve is almost identical to SP 57-3 in spite of the great apparent difference of site. Both stands have a severe water and nutrient regime, however, which is probably responsible for the similarity of niche space occupation pattern.

The very flat curve which indicates random distribution of ecological niches does not occur among the samples from KF and transitions to MDF in Fig. 8. Even the flat-test curve (SP 16) agrees with the lognormal pattern. The same applies to the curves of stands 15 in Fig. 9. The nearest approach to random distribution shows SP MA in Fig. 9 which gives relative biomass dominance in the mixed stand on terra firme near Manaus, Amazonia. The very small minimum sampling size expanded the right tail of the curve strongly, but hardly affected the main part of the curve.

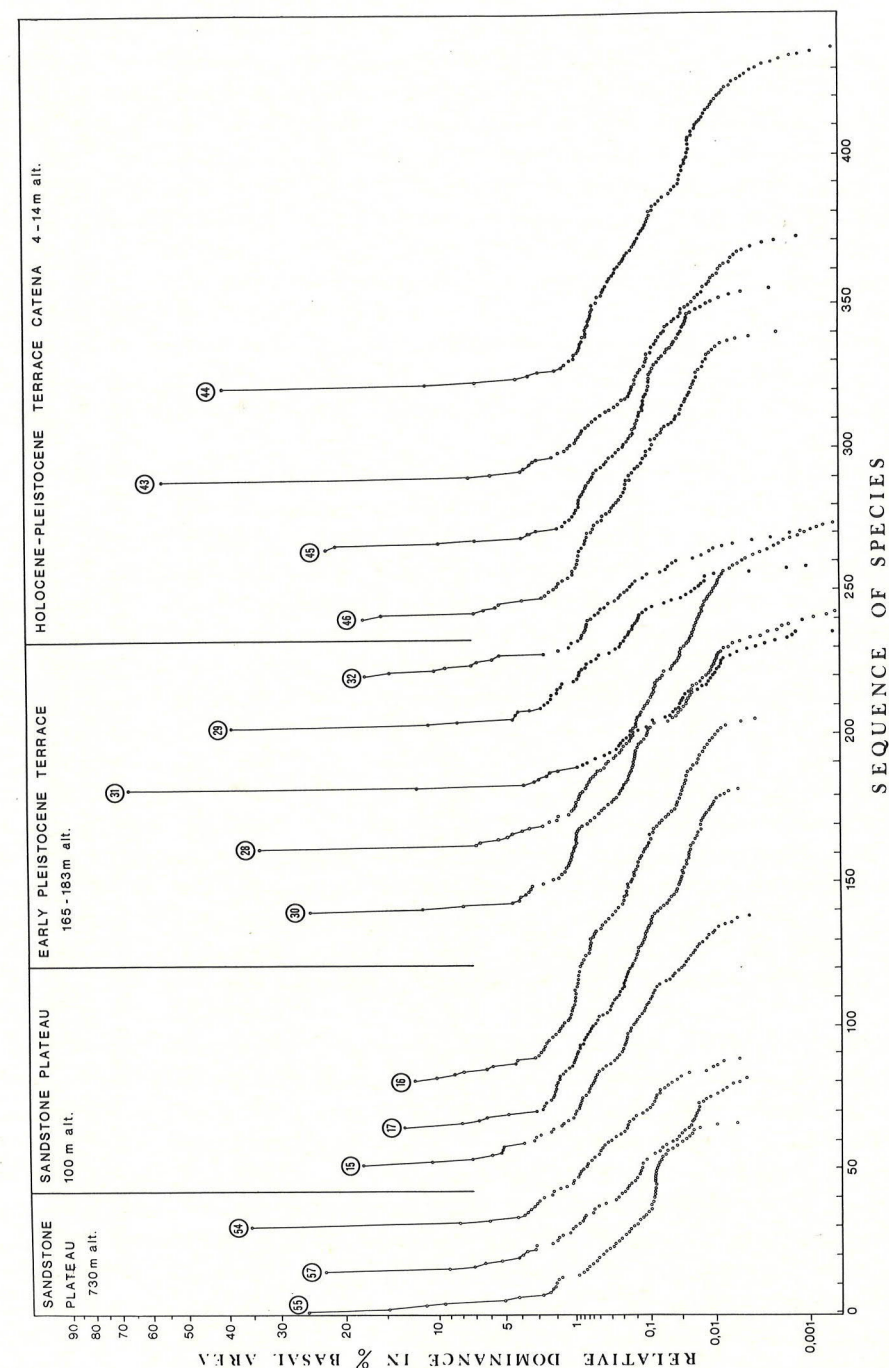


Fig. 8. Relative dominance-diversity curves of stands in catenas on different geological formations.

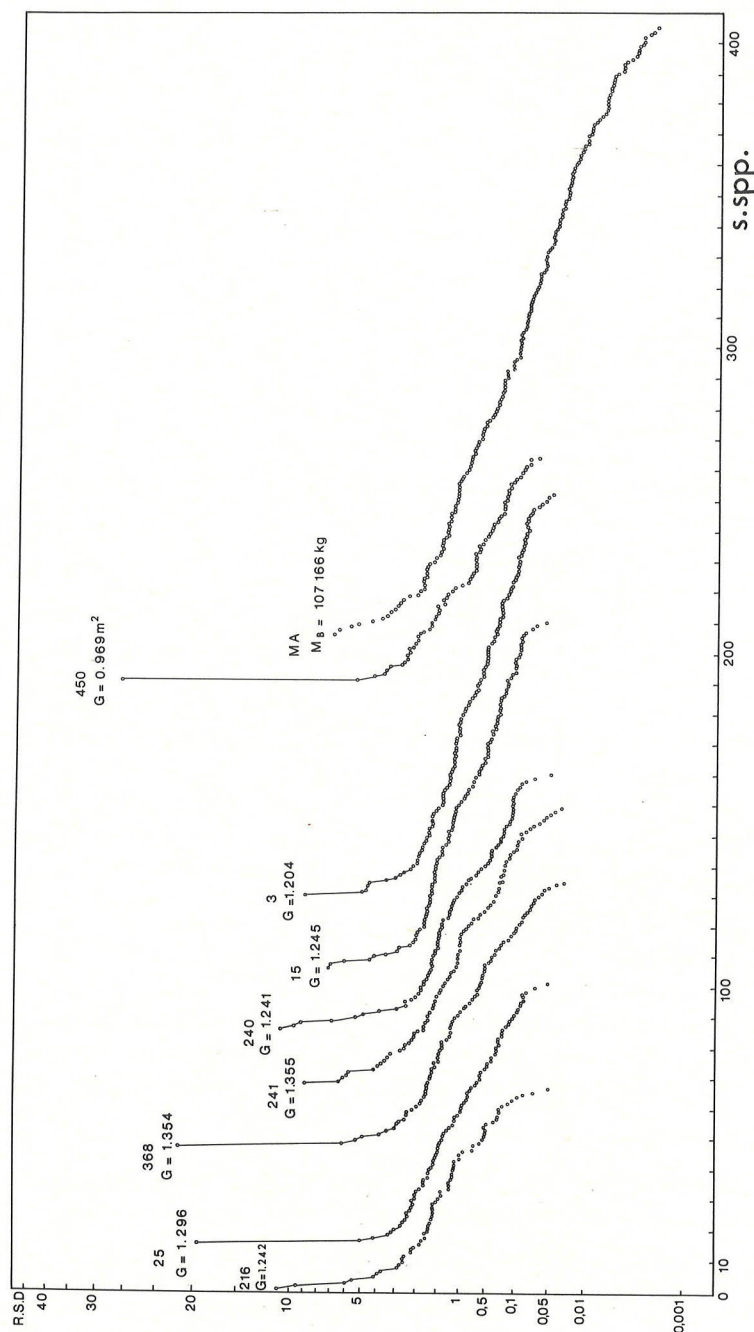


Fig. 9. Relative dominance-diversity curves of stands on different soil types in the Sabal sampling area (216 to 450). G = basal area in m²/405 m². Approximate hectare values can be calculated by multiplying by 25. MA = sample from the biomass plot near Manaus, representing a tree biomass of 107 t above ground (preliminary data from H. KLINGE).

The curves in Fig. 8 become steeper with greater severity of site conditions. Superimposed on this trend is a change with successional status. On the high-altitude sandstone plateau, curves become slightly steeper from well-drained riverside peat (SP 55) to raised bog (57) and blancet peat (SP 54). Within the peat bog in SP 57 the slope of the DD curve becomes a little steeper from the perimeter (SP 57-3) toward the centre (SP 57-2 and -1). A similar trend appears in the DD curves of the stands along the pleistocene terrace catena (SP 30 to 32). On the lowland sandstone plateau, the curve on SHP (SP 15) is steeper than in secondary KF on a secondary MHP (SP 17) or in a transitional stand to MDF on a MHP (SP 16). The small difference between SP 16 and 17 is unexpected. In comparison, SP 17 has a lower diversity value by individuals (Fig. 5) but a very high relative diversity value by basal area (Fig. 6). This indicates that the original dominance pattern is almost restored, while species richness and abundances of the species still deviate from the condition in a mature virgin stand. The DD curves of SP 16 and 17 would then be more similar than their McINTOSH values.

The features of the DD curves agree well with the relative DI values of the stands in Figs. 5 and 6. The similarity of the mid-sections of the DD curves of SP 31, 29 and 32 in Fig. 8 corresponds with their clustering in Fig. 5. The DD curves of SP 31 and 29 show strong single-species dominance and a steep mid-section. Their basal - area DI values in Fig. 6 are correspondingly low. The relatively strong dominance of the leading species in SP 28 causes a steep initial slope of the DD curve, but the flat mid-section indicates high diversity among the intermediates. As a result, SP 28 has a higher value than SP 30 or 31 in Fig. 6 a, but an equal position to SP 31 in Fig. 6 d due to the greater sensitivity of the IC index to dominance pattern.

In the coastal terrace catena, SP 45 and 46 have relatively flatter curves. This is possibly related to the immature phase of site and stand development and the corresponding rapid rate of change, and to the balanced water regime. The steeper initial slope and mid-section in SP 43 expresses the high degree of ecological stress on this site, which has been described earlier. The result is a tendency to pronounced dominance. The DD curve of SP 43 is rather similar to SP 31, which also has a similar DI value (Fig. 5). The DD curve of SP 44 is again flatter, which agrees with its higher DI value in Fig. 5.

The DD curves of the 8 transects in the Sabal sampling area differ noticeably in dominance pattern, which appears again related to soil type (Fig. 9). All curves are truncated at the lower end, because many small-sized rare species are excluded by the relatively high minimum sampling limit of 10 cm diameter, which corresponds to a lowest possible relative dominance value of about 0.05%. The curve of transect 216 on the poorest SHP has the steepest average slope but no pronounced single species dominance. The single species dominance and mid-section diversity both increase on the somewhat better SHP in transects 25 (10 YR 7,5/2) and 368 (10 YR 7/2). The single-species dominance decreases again but diversity in the mid-section remains relatively high on the MHP in 241 (10 YR 7,5/2,5) and in 240 (10 YR 5,5/3,5). The following two transects 15 and 3 are on RYP and the stands transitional to MDF. The initial slope is similar to that of the previous 2 lines, but the diversity among species in the mid-section of the

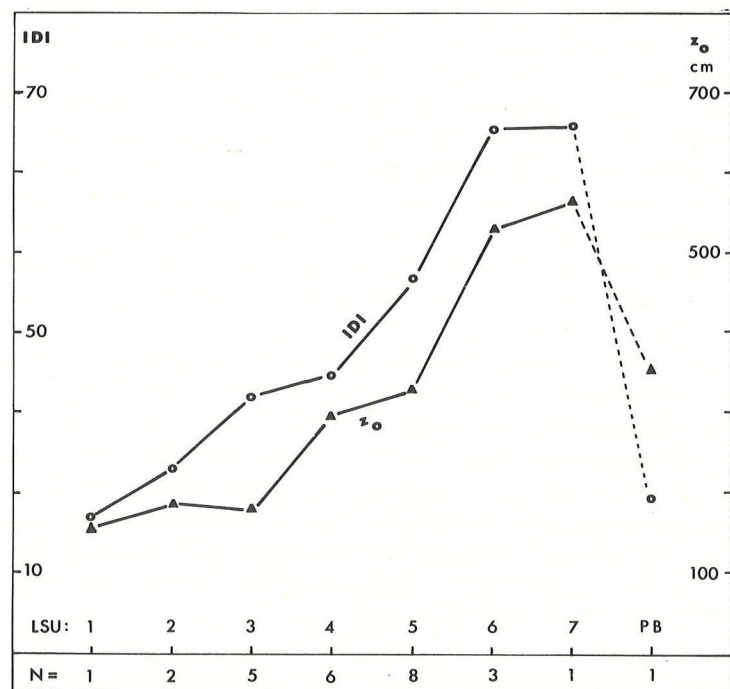


Fig. 10. The integrating combined diversity index (IDI) and the estimated aerodynamic roughness (z_0) of the canopy of 27 stands in 7 site units (LSU) and in a secondary Kerangas (LSU 1).

- 1 Secondary Kerangas (KF) on secondary humus podzol (HP)
 - 2 Peat bog on pleistocene terrace
 - 3 HP and grey-white podzolic soils (GWP) with strongly fluctuating water regime on pleistocene terraces and tertiary plateaux
 - 4 Moist HP and GWP on pleistocene and holocene terraces
 - 5 Moist loamy to clayey HP and GWP on tertiary sandstone slopes
 - 6 Wet but well-drained GWP on encased terraces
 - 7 Red-yellow podzolic loam on tertiary sandstone
- PB Groundwater HP transition to peat swamp
N Number of stands in LSU

curve is noticeably larger, especially in 3 on a deep RYP (10 YR 7,5/6). Also in MDF but distinguished by the high degree of dominance of a single Dipterocarp species (*Dryobalanops beccarii*) is transect 450 on a reddish-yellow clay (9 YR 7,5/8). The shape of the DD curves in SA 241, 3 and 450 agrees well with the DI values of these stands in Fig. 5.

3.4. The integrating index of diversity

The comparison of site pattern and features of the species-area lines suggested that site heterogeneity affects stand diversity on a very small scale. An index of diversity was therefore constructed, which combines number of species in the whole sample plot (0,2 ha) as a percentage of all species in the kerangas subformation, the tangent of the species-area line on semi-logarithmic paper, and the variation coefficient about this line. The index reads

$$IDI = Spp \% + (100 \tan) + SD \%$$

and integrates the effects of species richness, species pattern, and site heterogeneity. It is not independent of sample and plant sizes. Therefore, its usefulness is limited to the comparison of stands of equal area and similar plant sizes. Otherwise, the index is a useful measure for ranking stand ecosystems according to their overall diversity. For small forest areas, such as transects of 5 square chains, the index expresses primarily within-stand diversity. As additional areas are added and site heterogeneity increases, between-stand diversity affects the index more strongly. The usefulness of this index ceases if the species-area relationship deviates too strongly from the straight line (comp. section 2.2.).

The IDI values have been calculated for 27 sample plots (BRÜNIG, in print). The values were grouped in 7 land form-soil units. The mean IDI values increase with site quality from peat bog (LSU 2) through sandy (LSU 3 to 4) and clayey (LSU 5) podzols to well-drained GWP (LSU 6) and finally to RYP soils (LSU 7) in the transition to MDF (Fig. 10). The stand PB is the single-dominant stand (*Shorea albida* Sym.) in SP 27 on a peaty GHP in the transition to peat swamp. LSU 1 is the secondary KF in SP 17 on a secondary MHP. Both stands have few species, flat slope, and close fit of the species-area line in Fig. 2.

The structural properties of the stand canopy can be summarily represented by the indicator of aerodynamic surface roughness z_0 (SCHOLZ, in preparation). The aerodynamic surface roughness is proportional to the gradient of the wind profile and positively related to surface drag, turbulent exchange, external diffusion resistances, size of exchange surface, and radiation load on individual roughness elements in the canopy (BRÜNIG 1970). It is therefore an indicator of the stresses acting on the ecosystem surface from the atmosphere. Consequently, it is subject to limiting site conditions. Due to its derivation from canopy statistics (see Fig. 4 and BRÜNIG 1972 b), it is also a general measure of structural diversity of the stand canopy. The close correspondence of the IDI and z_0 in Fig. 10 agrees with the expectation that the structural diversities of floristic and morphological patterns of virgin forest stands are sim-

ilarly related to site quality, especially water regime. The ecologically better sites put less external stresses on the system and structural complexity is therefore less restricted. At the same time, niche space is less restricted.

The positions of IDI and z_0 are reversed in LSU PB (SP 27). This apparent contradiction is related to the high coverage of *S. albidia*, which dominates the tall, large-crowned top canopy of the stand. The very large albedo of the species compensates for the effects of the relatively great surface roughness and great height of the canopy, which otherwise would expose the system to severe stresses during drought periods. The low IDI and z_0 in LSU 1 are explained by the secondary nature of the stand. The species richness is still low and the top canopy has not yet developed the degree of complexity which would be expected on the site in a primary stand.

4. DISCUSSION

The hypothesis, based on the arguments of ASHTON (1969), BRÜNIG 1969; 1971), and BAILLIE (1972), is that the variation of soil conditions at micro-scale in the order of a few metres contributes to the size of niche space, but that environmental conditions such as the water regime restrict the availability of this space. Consequently, sites with a balanced water regime would provide a larger niche space than those on which ecological stress is caused periodically by prolonged excess or deficiency of water in the soil. If this is so, the forest vegetation should have more tree species and a higher degree of diversity on sites with more balanced water regime. Furthermore, stand diversity measures should show a relation to site heterogeneity, which should be more noticeable on better sites with less severe stresses. Species richness, equitability, and species distribution should therefore be related to soil conditions.

WONG and WHITMORE (1970) studied the species distribution pattern in relation to soil series in an area of MDF in Malaya. The topography was mostly flat and the soils either wet alluvials or clayey lateritic soils with varying degree of groundwater influence, derived from interbedded shales or granite. In an ordination of the stands, they found no evidence for narrow site tolerance of species such as reported by ASHTON (1964) from Brunei and by POORE (1968) for the rarer species in MDF in Malaya. WONG and WHITMORE point out that their linear plots cut across species clusters and that the analysis only takes account of presence or absence of species which limits the information value for the study of the problem of species distribution pattern.

A preliminary test for the distribution of density (N) and coverage (G) of 22 leading species in the Sabal sampling area produced strong evidence of a close correlation between N or G and the values of the MUNSELL soil colour notation. Correlation, aggregation, and association are now further tested for common and rare species. Additional information on the effect of soil variation on species distribution is expected and will be reported elsewhere. Results so far seem to give further support to the hypothesis that niche space is restricted by environmental factors in KF and that species distribution is influenced by relative minor and small-scale differences in soil conditions.

The larger coefficient of variation about the species-area lines on deep soils with balanced water regime accords with the hypothesis that niche space is larger in MDF than in KF or in PSF. The steeper slope and eventual up-turn of the species-area line also suggest a continued increase of niche space on the ecologically better sites (Figs. 2 and 3). The consistent change of species richness and diversity along transects in relation to depth, texture and chroma of the soil, to the degree of sloping of the site, and to the phase of paludification suggest that soil conditions in fact influence niche space. One of these effects is a noticeable and consistent site-related between-stand diversity pattern at very small scale.

The co-ordinates by McINTOSH index values (y axis) and species richness (x axis) are lower on mineral soils with imbalanced water regime and on peat bogs, where the tendency for dominance by one or a few species is high (Fig. 5). Substitution of G for N accentuates this trend (Fig. 6 a). The relative DI values as a percentage of the maximum are less affected and show distinctly lower values only on sites with unusually high single-species coverage (Fig. 6 c). The IC values also decline generally with the severity of the environment and the maturity of the stand, but the relatively very high sensitivity of the IC index to dominance patterns may cause aberrant values and difficulties in ecological interpretation. The general conclusion from the trends of DI and IC values is that obviously better adapted species are relatively more successful in exploiting the niche space if this space is restricted by ecological stresses. Consequently the diversity and the average information content of the stand will be reduced.

In terms of dominance, this means that the better adapted and more successful species contributes a larger portion to the stand basal area. Successful adaptation and reproduction leads to the gregariousness which is typical of many species and site types in PSF, KF (Fig. 9, transects 25 and 368) and occasionally in MDF (Fig. 9, transect 450). High coverage by gregarious species causes a steep initial slope of the DD curve. The length and steepness of the mid-section of the curve is an efficient measure of the floristic diversity of the stand. The majority of species in this section are intermediate (B layer) and mid-storey (C_1 layer) trees. Therefore, diversity among trees below the top canopy layer is inversely related to the steepness of the mid-section. If a high degree of diversity in the lower strata is an adaptive feature to conserve nutrients (KLINGE and FITTKAU, elsewhere in this issue), the low-diversity stands on the most nutrient-deficient soils must be otherwise adapted. It might be speculated that the high degree of evergreenness and the low rates of productivity on these soils are such adaptive features (BRÜNIG, in print).

Stands with curves with a relatively short and flat initial section and a long, flat mid-section also have a high DI value and a steep species-area line with a high variation coefficient (Figs. 3 and 9). A generally steeper DD curve, on the other hand, has a smaller initial species number, a flatter slope and a lower coefficient of variation of the species-area line. At the same time, the values of the IDI and z_0 as measure of structural diversity are correspondingly lower, which points to a close relationship between floristic diversity, structural diversity, and amount of environmental stress. This relationship is so close that

stands on ecologically similar sites are similarly structured even if their species complements consist of different taxa at species level to such a degree that the stands occupy widely separated positions in an ordination according to their floristic similarity.

5. CONCLUSION

The large degree of coincidence between variations in floristic and structural statistics and features of the soil, and site and the successional status of the vegetation-site complex, make it very likely that site factors play an important role in determining species richness and diversity of floristic and morphological structures of forest stands in the equatorial perhumid evergreen lowland forest. This applies to areas as small as 0.2 ha as well as to larger tracts of land. On the better sites, such as average MDF and the best KF sites, indications are that the joint action of a great number of environmental factors is largely responsible for defining and delimiting available niche space and individual species niches. On the poor sites, certain environmental factors severely limit available niche space. Gradient analysis has indicated that the nature of the water regime and, to a lesser degree, nutrient availability on the site, may be the main causal factors (BRÜNIG, in print). This agrees well with the assumption that the richness of species in equatorial lowland forests is positively related to the absence of severely limiting environmental events, such as drought, waterlogging, or alternation between the two, which eliminate the effect of minor site differences in shaping available niche space.

The observed limitations of the floristic and structural diversity of mature natural forest vegetation by site conditions have considerable practical significance. Forestry and landscape planning and management must observe these limits if stability and utility of stand ecosystems and the landscape as a whole are desirable objectives. Exceeding these limits as a result of poor planning will necessarily lead to failure through instability or to excessive costs through loss of utility or through additional inputs which become necessary to enforce a naturally lacking stability.

SUMMARY

Site conditions in the Mixed Dipterocarp forests of Sarawak and Brunei are characterised by the absence of prolonged drought. This permits minor site differences to become ecologically fully effective. In the kerangas forests, drought conditions occur frequently and regularly. An extremely variable water regime and uniformity of chemical and physical soil conditions are typical of kerangas peat bogs and deltaic peat swamp forest sites. Consequently, fewer niches are available and the number of species is less on these sites than in Mixed Dipterocarp forest. Upland kerangas sites are intermediate in this respect. About 850 tree species (428 genera) are recorded from kerangas forests. It is estimated that the total number of tree species in all forest types in Sarawak and Brunei is between 2 500 and 3 000, and 2 800 and 3 300 respectively.

The positions, shapes, and variation coefficients of the species-area lines are strongly influenced by conditions of soil and physiography. The diversity index of McINTOSH

and the average information content indicate a high degree of diversity among trees of stands on sites with balanced water regime. Low values occur in late phases of peat development and on sites with frequent droughts or with alternating dry and waterlogged conditions. The differences are accentuated if the basal area is substituted for number of individuals in the index.

The shape of the dominance-diversity curves according to WHITTAKER indicates that on favourable sites a great number of environmental factors determines the diversity of ecological niches. On less favourable sites, niche space appears to be restricted by environmental severity, and a tendency to dominance and reduced species diversity is evident.

The values of an integrating index of diversity are related to soil-landform units which reflect ecological gradients primarily related to the water regime. The trend of the index values agrees with the trend of structural complexity expressed as estimated aerodynamic surface roughness.

A synoptic assessment of the various indicators of diversity suggest the important role which environmental factors play in shaping ecological niche-spaces in the equatorial lowland forests.

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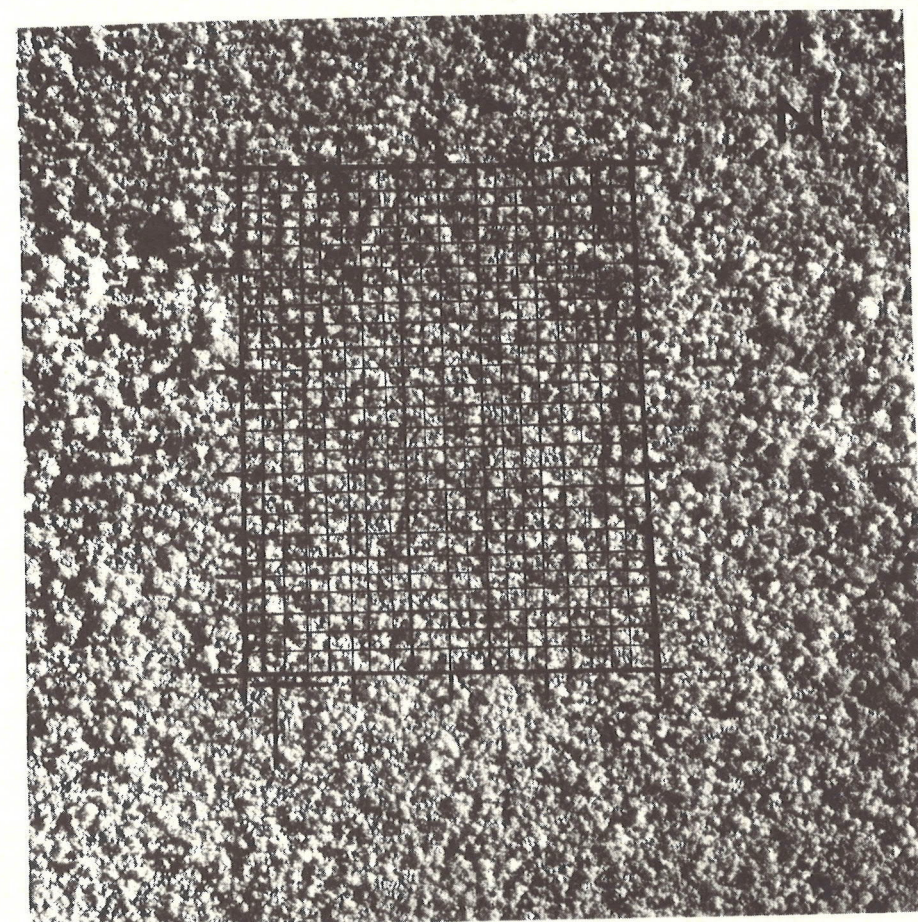


Plate 1. Aerial view of the pattern of canopy surface morphology in the Sabal sampling area. To the left and right of the sampling area (400 x 500 m grid of 500 squares) is the large-crowned, rough and irregular surface of Mixed Dipterocarp forest. The pattern within and south of the sampling area is an intricate mixture of kerangas stands of different roughness according to site conditions. Sarawak Government copyright.

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